Ornithological research in tropical America — the last 35 years

by D. W. Snow

A major part of the research literature on tropical American birds is published in American journals, and for this reason is not as well known to European ornithologists as it might be. And for obvious reasons – geographical proximity, and the large number of active ornithologists based on universities and museums – the American contribution is likely to preponderate still more in the future. Most of the research is biological – that is, it deals with the ecology and behaviour of birds; it is no longer a matter of simply describing and cataloguing. A hundred years ago the position was very different: European ornithologists were then in the forefront, most of the bird species had been discovered and their geographical variation was beginning to be worked out, but biological studies were still far in the future. The change of emphasis, which coincides closely with the end of the last World War, provides a convenient starting point for the present review.

The aim of this paper is to draw attention to some of the newer developments in tropical American ornithology, especially for readers who have not had access to the large and scattered literature. The topics dealt with inevitably reflect to some extent a personal bias; but some of them, at least, would take a prominent place in any review of the subject. Some topics – notably migration and breeding seasons – have been omitted, for various reasons. Migration within South America is still very little understood; it has been reviewed by Sick (1968), but few recent advances have been made, and nothing comparable to what is now known of the migration of African birds within Africa. Breeding seasons and annual cycles have been investigated in detail in a few areas, but no general synthesis has been made; and information for large areas at low latitudes, especially the Amazonian forest, is very sparse.

Ornithological exploration

The pioneering stage in the ornithological exploration of tropical America, by expeditions and professional collectors financed by European and North American museums, ended with the second World War. By the end of this stage the foundations of knowledge of the distribution and geographical variation of the Neotropical avifauna had been securely laid. The results were brought together in the monumental *Catalogue of Birds of the Americas,* published between 1918 and 1949, a work which is still the starting point in any serious avifaunistic research. Ornithological exploration has continued since then, but it has in the main been differently organized. Traditional exploration has been continued on a regional basis by the major South American museums, including the private Phelps Museum in Venezuela (which is shortly to become the Venezuelan national ornithological collection). As a result many gaps in knowledge have been filled in, and Venezuela in particular, an extremely rich country which had been neglected in the earlier years, has now one of the best known avifaunas. In addition to locally based exploration of the traditional kind, a number of more or less long-term

field stations have been established (some based on existing institutions), and these have resulted in very detailed knowledge of local avifaunas. Examples are Rancho Grande in Venezuela (cloud forest of the coastal cordillera), the Museum Goeldi in Brazil (lowland forest of lower Amazonia), the Rio Palanqui Research Station in Ecuador (humid forest on the western slopes of the Andes), and Cocha Cashu Station in the Manu National Park in Peru (lowland forest of upper Amazonia). In the last of these, over 470 bird species have been recorded within 5 km of the Station, making it the richest forest area known in the world.

Outstanding among the intensive regional surveys has been the work of members of the Louisiana State University's Museum of Zoology, who since 1961 have been working in the Peruvian Andes and at the base of the Andes on the eastern side. This geographically complex area has produced an extraordinary succession of new species, many of them very distinct. When the last was described (*Xenoglaux loweryi*, a tiny owl with several peculiar features including a very reduced sternal carina – O'Neill & Graves 1977), the score stood at 21 new species, 4 of which have been placed in new genera; and there are certainly more to come. The wealth of this area may be better appreciated when it is compared with the rest of the continent. In the years 1941–1965 20 new species were discovered in other parts of South America. They include no new genera; only a few of them are at all distinct from known species, and most can reasonably be included as allospecies (geographical representatives), or even subspecies, of species already known (Mayr 1957, 1971). It is especially noteworthy that the continuing ornithological exploration of the Andean slopes of Ecuador, Colombia and Venezuela has produced nothing comparable to Peru. When the Peruvian discoveries have been completed (if they ever are) it will be a fascinating task to analyse them in relation to the rest of the South American avifauna and to what is known of past climatic and geological changes. Does this area harbour, in addition to more recent elements, a relict avifauna which has disappeared from the rest of the continent?

Avifaunistic analyses

The tropical American avifauna is now sufficiently well known for zoogeographical analysis, and an increasing number of such studies have appeared in recent years. Vuilleumier (1969 a, b) examined geographical patterns of differentiation and speciation in Andean birds; Mayr & Phelps (1967) analysed the endemic birds of the Guiana highlands (for which they coined the name "Pantepui") and discussed their origin; and Short (1975) analysed the avifauna of the *chaco* region, the well-defined block of arid woodland in Paraguay, Bolivia and northern Argentina, and related it to the avifauna of other arid woodland areas of the continent. Perhaps the most fruitful studies, however, have been Haffer's analyses of speciation patterns in tropical forest areas, especially Amazonia (Haffer 1970, 1974; Simpson & Haffer 1978). Haffer's main thesis is that during arid periods in the Quaternary (probably contemporaneous with glacial periods in the north) the Amazonian forest was reduced to a number of isolated pockets or "refuges" (corresponding to areas where rainfall is especially high today), that the isolated sections of species thus split differentiated from one another under the differing environmental influences to which they were subjected, and that when the forests

subsequently spread with the return of more humid conditions the isolated populations spread with them and came into contact again. When they came into contact various outcomes were possible, depending on the degree of differentiation and reproductive incompatibility achieved in isolation. Haffer's hypothesis provides a convincing explanation of many present-day distribution patterns; it is particularly convincing in the case of groups of closely related species which abut on one another's ranges without any overlap (so-called "parapatric" species). This is a rather common situation in Amazonian birds. In such cases it seems that the species concerned have evolved effective isolating mechanisms preventing interbreeding, but are still too similar ecologically to be able to penetrate each other's ranges and coexist. In other cases more or less narrow zones of hybridization seem to mark the areas where formerly isolated forms, which have not achieved reproductive isolation, have come into contact again.

Haffer's hypothesis helps to explain Amazonia's great richness in bird species. It provides the element of geographical isolation necessary (according to generally accepted theory) for species formation. But it clearly does not go the whole way to explaining South America's extraordinary diversity of species. Geomorphological evidence will have to be taken into account. For instance, from the beginning of the Tertiary until the mid-Tertiary northern South America was represented by 3 separate land-masses: a northern Guianan region, a southern Brazilian region, and to the west an emergent Andean region (Simpson & Haffer 1978). The present Neotropical avifauna must have been formed by a fusion of the avifaunas of these 3 areas, with a further contribution from North or Central America (Mayr 1964).

Species studies

There have been a considerable number of these, but the number of species dealt with is still a tiny fraction of the whole. William Beebe, working mainly in British Guiana (now Guyana), and Frank M. Chapman, working on Barro Colorado Island in Panama, were the 2 pioneers. Since their time, 4 long-term residents have added greatly to our knowledge of individual species. In Central America, Dr A. F. Skutch has produced a volume of publication on the biology, especially the breeding, of single species that is unrivalled in quantity and in the length of period of sustained publication (1930 to the present). His studies have been brought together in several books, in addition to papers in journals, the greatest number in 3 volumes of the Pacific Coast Avifauna series published by the Cooper Ornithological Society. Dr H. Sick, long resident in Brazil, has contributed greatly to knowledge of the birds both of Amazonia and of eastern Brazil; among his many notable discoveries may be mentioned the nest of the Amazonian Umbrellabird *Cephalopterus ornatus* (Sick 1954). F. Haverschmidt, resident in Surinam from 1946 to 1968, added greatly to knowledge of the feeding habits and breeding of birds in that country. P. A. Schwartz, resident in Venezuela from the early 1950s until his sudden death in April 1979, produced many important contributions to the biology of a wide range of species, from tinamous, hawks and toucans to finches and manakins. His death cut short an ornithological career that was approaching its peak of productivity, and tragically much partially completed research of the greatest interest will now remain unpublished.

Single species studies in depth have also been made by ornithologists temporarily resident at field stations. Dr E. O. Willis, working in several different areas from Panama to Brazil, added tremendously to our knowledge of antbirds and other species that accompany army ants. The studies by my wife, Barbara K. Snow, and myself in Trinidad, Guyana and other parts of northern South America have been concerned mainly with cotingas, manakins, hummingbirds and the Oilbird *Steatornis caripensis*. In studies such as these there has understandably been some bias towards species which are reasonable easy to locate, especially those that have fixed display areas or smallish territories in the lower strata of the forest. This has, in fact, meant that a great deal of attention has been given to lek birds, and one outcome of this has been to emphasize an important difference between Neotropical and African forest birds. There are apparently no lek species in the African forest avifauna, and this is probably related to the comparative rarity of specialised frugivores in Africa, which in turn is related to the comparative poverty of the African forest flora (Snow 1979).

Population dynamics

A few long-term studies based on colour ringing have begun to give estimates of annual survival of forest birds. Calculation of survival rates from returns of ringed birds by members of the public, the usual method in Europe, is of course generally impossible in tropical America and out of the question for forest birds. Male Black-and-white Manakins *Manacus manacus* in Trinidad were found to have an annual survival rate of at least 89% (Snow 1962a), and an indirect estimate for the Golden-headed Manakin *Pipra erythrocephala* gave a figure of about 90% (Snow 1962b). These figures are remarkably high by comparison with survival rates of small passerines in temperate latitudes, but they seem to be well founded. Continued monitoring of the Trinidad Black-and-white Manakin populations over a further 10 years by Dr A. Lill (Snow & Lill 1974) gave an absolute minimum survival rate of 79%, based on recaptures. Allowing for individuals that there was good reason to suppose must have escaped capture, the true survival was probably substantially higher than 79%. The greatest minimum age at recapture for a Black-and-white Manakin was 14 years, and for a Golden-headed Manakin 12 years. The 14-year-old bird had probably been a continuous territory-holder at a lek for at least 11 years.

The only other figures available for forest birds are those obtained by Willis for 3 species of antbirds in Panama. The most complete data, for the Spotted Antbird *Hylophylax naevioides*, indicated an annual survival of 81.2%; for the two other species, *Gymnopithys bicolor* and *Phaenostictus mcleannani*, the figures were 71% and 70% respectively (Willis 1974).

Such high annual survival rates must mean that breeding success is very low, if the populations are to remain more or less stable; and in fact most studies have shown that a very high percentage of nests in American tropical forests fail. For the Black-and-white Manakin in Trinidad, only 19% of nests were successful (i.e. produced at least one young) (Snow 1962a), for the hummingbird *Glaucis hirsuta* 17% (Snow & Snow 1973), and for the thrushes *Turdus fumigatus* and *T. albicollis* 21% (Snow & Snow 1963). For the Spotted Antbird in Panama, Willis (1974) recorded a success rate of less than 13%. These and other figures based on smaller samples indicate that very low success rates are typical of tropical American forest birds.

Mixed species flocks

Foraging flocks composed of different species of birds are a feature of tropical forest in many parts of the world. A great advance in understanding their composition and function has resulted from recent studies in tropical American forests, especially those by Willis (1967, 1972, 1973) and Munn (1979). Willis worked out in great detail the social organization of 2 antbird species which are closely associated with army ants, accompanying them and feeding on the insects which they flush. He found that there is a system of overlapping home ranges. Each established pair owns a territory, but the territory is not exclusive: neighbouring birds are allowed to trespass, but they are subordinate to the owners. Thus as an army ant column moves on, passing from one pair's territory to another, different individual birds are dominant at the ant swarm. The social organization of antbirds that form mixed foraging flocks, unassociated with army ants, is quite different. The main species involved belong to different species from the army ant followers. In the flocks studied by Munn, in Peru, the permanent, core members belonged to 6 species – 2 (larger) species of *Thamnomanes*; and 4 (smaller) species, 3 of *Myrmotherula* and one of *Philydor*. Furthermore, each species was represented in each flock by an adult pair with their dependent offspring (if any), and the flock territory was defended jointly by all flock members. Munn's study showed that flock territories and composition remained remarkably stable over 2 years. It seems possible that over large tracts of Amazonia the population of these core species is regulated and kept uniform one with another by the permanent structure of their foraging flocks. It also seems likely that mutual warning against predators (the small forest hawks of the genera *Accipiter* and *Micrastur*) is the most important function of these flocks.

By comparison, the foraging flocks of tanagers, flycatchers, furnariids and other birds that move through the higher strata of the forest have remained little studied. It will be of great interest to compare these flocks, which are so much more difficult to observe and follow, with the mixed flocks at lower levels, and to compare all of them with the mixed feeding flocks of other continents, consisting as they do almost entirely of birds of different families.

Co-evolution of birds with other organisms

More or less specialised co-adapted relationships between birds and plants are perhaps more prevalent in tropical America than elsewhere. Two kinds of relationship are of prime importance: between fruit-eating birds and the fruits that they eat, and between nectarivorous birds and the flowers that they exploit.

Co-evolution between specialised frugivorous birds and the fruits that they eat has involved a few main plant families, especially the Lauraceae (laurels), the Palmae (palms) and Burseraceae (incense family). Trees belonging to these families bear highly nutritious fruits which can provide a complete, or almost complete, diet for specialised frugivorous birds such as toucans and cotingas. Specialised frugivores are reliable dispersal agents, as they depend on the fruits of particular kinds of tree. The tree invests a relatively large amount of its resources in each fruit, in the form of fats, proteins and carbohydrates, the high investment being the price that it pays for the services of reliable dispersal agents. Proof of these ideas is hard to obtain, but Howe &

Primack (1975) have shown, in a detailed study of seed dispersal from one tree, that the dispersal of its seeds to suitable habitats is more likely to result from the behaviour characteristic of specialised frugivores than from that of unspecialised opportunist frugivores.

Fruits adapted for dispersal by unspecialised frugivores belong to many different families, the 2 most important being the Melastomataceae and Rubiaceae. Plants bearing such fruits invest little of their resources in any one fruit; they mainly produce small succulent fruits (containing mainly sugars and little fat or protein), their strategy being to attract as many opportunist fruit-eaters as possible. The ramifications of these and other more subtle interactions between plants and frugivorous birds are only just beginning to be appreciated, and most of the research so far has been confined to tropical America (e.g. McKey 1975, Morton 1973, Howe & Estabrook 1977).

A large and fast-growing literature deals with the co-evolutionary interactions between nectarivorous birds and the flowers that they exploit. A great impetus to such research has come from the fact that the amount of energy offered by the flower (in the form of simple sugars), its rate of production, and the efficiency with which hummingbirds can exploit it are all measurable in the field under favourable conditions, while laboratory measurements are available for the metabolic rate of hummingbirds under various conditions. The results of this research cannot possibly be summarised in a few lines, and it may only be mentioned that a broad division has been established between 2 fundamentally different foraging strategies for hummingbirds: territoriality and "trap-lining". Territorial species are generally small to medium-sized hummingbirds with short, straight bills, which exploit small unspecialised flowers which are densely enough clumped to provide a defendable resource. Trap-liners are generally larger species with long, often curved bills, which exploit large flowers with long corolla tubes to which their bills are adapted. Such flowers are usually too sparse to provide a defendable resource, so that the trap-liner (as its name implies) has to move round a large circuit in order to fulfil its needs. The most recent research has shown that not only bill size and shape but also aerodynamic features (wing disc loading) are involved in adaptation for either the territorial or the trap-lining way of life (Feinsinger & Chaplin 1975, Feinsinger *et al.* 1979).

A quite different kind of co-adapted relationship, involving the association of nesting birds (several species of icterids and tyrant-flycatchers) with stinging or biting Hymenoptera, has been described by Smith (1968, 1979). Smith has shown that both partners in the association gain an advantage, the birds getting protection both from nest-predators and from bot-flies whose larvae attack the nestlings, and the insects getting protection against certain birds and mammals which specialise in eating their larvae. There is a further surprising complication in the case of those icterids that are parasitised by the cowbird *Scaphidura*. Nestling *Scaphidura* are very efficient at removing and eating bot-fly larvae from themselves and from other nestlings in the nest with them. Nests which are not protected by a wasps' nest thus benefit from being parasitised by the cowbird; but only if they contain a single young cowbird. If there are 2 or more young cowbirds in the nest they usually out-compete the host chicks for food, negating the advantage that they confer by ridding them of bot-fly larvae.

The tendency of certain birds to nest close to nests of stinging and biting Hymenoptera has been known for a long time. Smith's study, of which the above is a simplified summary, is the first to reveal the extraordinarily complex nature of such relationships.

Literature, and the amateur contribution

Nearly all the research to date on tropical American birds has come from professional ornithologists. There is no parallel to the amateur contribution that has made African birds so much better known than tropical American birds. For any amateur ornithologist visiting the region, the lack of adequate reference books has until recently been a major handicap. With the publication during the last few years of a number of excellent field guides and handbooks the situation is changing, and it may well be that significant additions to knowledge of Neotropical birds will begin to come from expatriates temporarily resident in little known areas and from amateur ornithologists making short visits with particular objectives. It is probably fair to say that short-term visitors making more or less casual lists of species observed are unlikely to add very much, as the avifauna of the more accessible areas is too well known for such records to be very significant. This is by no means true, however, of nesting, feeding habits, and other aspects of the biology of even the most common species.

For the visitor to any part of tropical South America, Meyer de Schauensee (1970) is of the greatest value, and indispensable for anyone visiting a country that has not yet got its own handbook. There are still only a few countries that have up-to-date handbooks or field-guides: Colombia (Meyer de Schauensee 1964, now out of print), Venezuela (Meyer de Schauensee & Phelps 1978), Guyana (Snyder 1966), Surinam (Haverschmidt 1968), and – zoogeographically part of South America – Trinidad and Tobago (ffrench 1973).

Central America is now well covered by up-to-date field-guides. The excellent book by Peterson & Chalif (1973) covers not only the birds of Mexico but all species found in Guatemala, British Honduras (Belize) and El Salvador. Most of the species in Ridgely (1976) extend west of Panama to Costa Rica and beyond. Thus Peterson & Chalif and Ridgely together include the great majority of Central American birds. The only field-guide that covers all Central American species is that by Davis (1972); but this work needs to be used with caution, as it contains many idiosyncrasies including much unorthodox taxonomy and nomenclature (see review by Parkes 1973).

Finally mention should be made of a major new work of reference by Emmet R. Blake, *Manual of Neotropical Birds,* to be completed in 4 volumes, of which the first has already appeared (Blake 1977). When complete, this will to a large extent replace the *Catalogue of Birds of the Americas* for the student of Neotropical birds, and for the foreseeable future will remain the standard work on the distribution, description and taxonomy of Neotropical birds. It does not include data on ecology or behaviour, but gives references to the main publications that are available on the life history of each species.

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Kale, Herbert W. (Editor). 1979. *Rare and Endangered Biota of Florida. Vol.* 2. *Birds.* Pp. 121. Black-and-white photographs. Soft covers. University Presses of Florida. 7 dollars.

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